

## The functional significance of medially divided cribella in the spider genus *Mallos* (Araneae, Dictynidae)

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### Summary

A transformational analysis that includes four species of *Mallos* with entire cribella and two species with medially divided cribella shows that cribellum width, surface area, and spigot number are correlated with carapace width. There is no evidence that these relationships differ between species with entire and divided cribella. Thus, in *Mallos*, a median cribellar division does not appear to be associated with changes in cribellum features that are known to increase the stickiness of cribellar threads.

### Introduction

The cribellum is an oval spinning field situated on the ventral surface of a spider's abdomen, just anterior to its spinnerets. This plate bears thousands of spigots, each of which contributes a small fibril to the spider's cribellar prey-capture thread (Opell, 1994; Peters, 1984, 1992). These fibrils are drawn from the cribellum by a setal comb, termed the calamistrum, located on each of the spider's fourth metatarsi (Eberhard, 1988). In the finished cribellar thread these fibrils form a loosely packed cloud of dry, looped fibrils that surround two or four supporting axial fibres (Eberhard & Pereira, 1993). The stickiness of cribellar thread is directly related to the number of spigots on the cribellum that produced it (Opell, 1994, 1995).

The cribellum is a synapomorphy of the Infraorder Araneomorphae, where it first appeared as an oval plate (Platnick, 1977; Forster *et al.*, 1987). However, in some araneomorphs the cribellum is divided medially (cf. Figs. 1 and 2). Not surprisingly, the division of the cribellum has served as a character in spider classification (Lehtinen, 1967). In some families (e.g. Filistatidae and Deinopidae), all members have a divided cribellum, whereas in others (e.g. Hypochilidae and Uloboridae), all members have an undivided cribellum. However, there are families (e.g. Dictynidae) that contain some genera with an entire cribellum and others with a divided cribellum. The dictynid genus *Mallos* O. Pickard-Cambridge, contains 10 species that have an entire cribellum and four species that have a divided cribellum (Bond & Opell, in press). Thus, the median division of the cribellum appears to be a rather plastic feature.

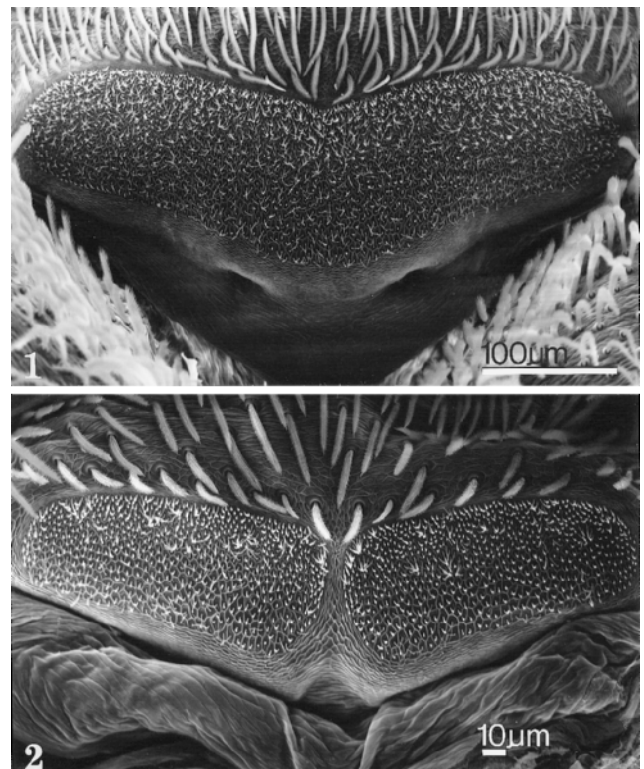
Little is known about the functional significance of a divided cribellum. As the cribellum is responsible for producing a spider's prey-capture thread, it may be that a divided cribellum facilitates the spinning of cribellar threads, or increases the stickiness that is achieved by a given number of cribellar fibrils. The number of spigots that form a spider's cribellum is the major determinant of the stickiness of its cribellar threads (Opell, 1994). Cribellum width is also positively correlated with

cribellar thread stickiness (Opell, unpublished results). However, changes in spigot density, calamistrum features, and probably spinning behaviour can optimise cribellar thread stickiness (Opell, 1995).

This study compares the cribellum features of four *Mallos* species that have entire cribella and two that have divided cribella. It tests the hypothesis that a divided cribellum is associated with an increase in cribellar thread stickiness, as gauged by greater weight-specific cribellum width, surface area, and spigot number. The species *Mallos dugesi* (Becker) and *Mallos blandus* Chamberlin & Gertsch have a plesiomorphic, entire cribellum (Fig. 1). The other four species belong to a clade for which a medially divided cribellum (Fig. 2) is a synapomorphy (Fig. 3). In this clade, *Mallos pallidus* (Banks) and *Mallos niveus* O. Pickard-Cambridge have a divided cribellum, but *Mallos pearcei* Chamberlin & Gertsch and *Mallos mians* (Chamberlin) have a secondarily entire cribellum. Thus, the species included in this study represent a section of the *Mallos* clade where cribellum division appears to be very plastic.

### Methods

Five mature females of each species were measured. Maximum carapace width was used as an index of spider size. We removed each specimen's cribellum, mounted it on a microscope slide in water-soluble mounting medium, and measured cribellum width and surface area under a compound microscope equipped with differential phase contrast and connected to a computerised digitising apparatus. Total number of spigots on the



Figs. 1–2: Scanning electron micrographs of the entire cribellum of *Mallos dugesi* (1) and the medially divided cribellum of *Mallos niveus* (2).

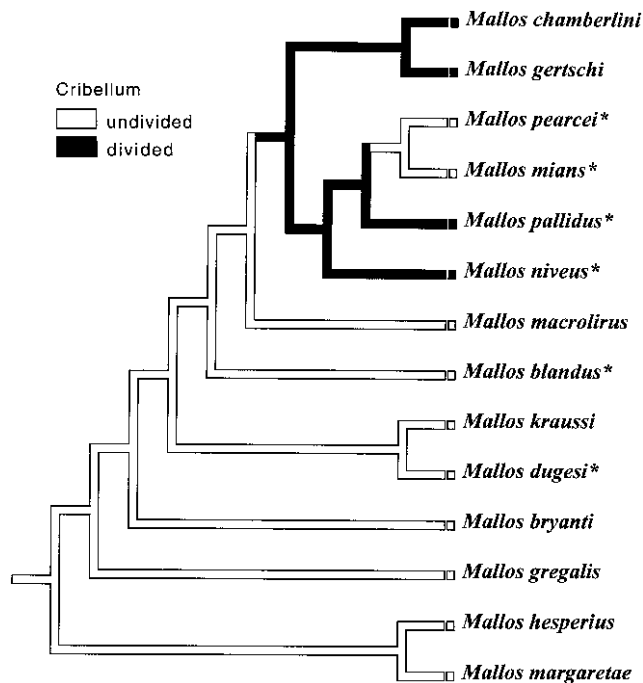


Fig. 3: Phylogeny of *Mallos* species from Bond & Opell (in press), showing those species with entire and divided cribella. An asterisk denotes those species included in this study.

cribellum was determined by multiplying the cribellum's surface area by its mean spigot density, as described more fully by Opell (1994).

Bond & Opell (in press) propose a phylogeny for the genus *Mallos* based on 26 morphological characters. One of these characters was the presence or absence of a median cribellar division. To obtain a phylogeny that was independent of the character we wished to evaluate, we excluded this character from a reanalysis of the relationships of the 14 *Mallos* species. The computer program PAUP (Swofford, 1991) produced a tree that was nearly identical to that proposed by Bond & Opell (in press), the only exception being that resolution was lost in the *M. niveus* subclade. Therefore, we accept the original tree topology (Fig. 3) as valid for testing questions about the evolution of cribellum features.

Parametric statistical tests assume that observations are independent. This requirement makes it

inappropriate to examine character evolution in related taxa with typical regression techniques. For a number of reasons (Felsenstein, 1985; Harvey & Pagel, 1991), one would expect more closely related species to have more similar values. Therefore, we used the methods described by Huey & Bennett (1986, 1987) to evaluate the evolution of continuous characters. This method infers the ancestral character states of species, calculates changes from these states to those of extant species, and examines correlations between the changes in characters that are hypothesised to be associated (Opell, 1994). Ancestral character states were computed using the squared change parsimony algorithm of the computer program MacClade ver. 3.0 (Maddison & Maddison, 1992). Squared change parsimony minimises the sum of the squared changes on the branches (Maddison, 1991).

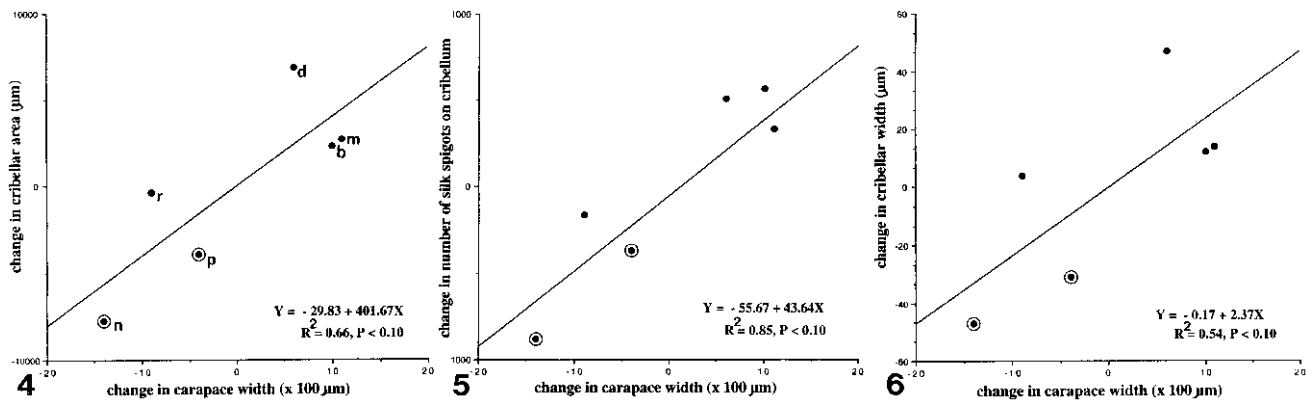
## Results and Discussion

Table 1 presents the mean values of the six species and the values at their ancestral nodes. Regression analyses show that all cribellum features are correlated significantly ( $p < 0.10$ ) with carapace width. Change in cribellar area regresses against change in carapace width ( $F = 7.70$ ,  $p = 0.05$ ; Fig. 4). Change in spigot number regresses against change in carapace width ( $F = 23.17$ ,  $p = 0.009$ ; Fig. 5). Change in cribellum width regresses against change in carapace width ( $F = 4.65$ ,  $p = 0.097$ ; Fig. 6). As only two species with divided cribella are included in these analyses, it is not possible to use other statistical tests, such as analysis of covariance, to compare the regressions of species with entire cribella to those with divided cribella.

In the genus *Mallos*, a medially divided cribellum is not associated with an increase in cribellum width, surface area, or spigot number, features that would suggest that a divided cribellum directly increases cribellar thread stickiness. However, a median division may enhance the stickiness of cribellar thread in other ways. It may cause the two halves of the cribellum to lie in different planes and, thereby, change the angle at which

	Carapace width (mm)	Spigot number	Cribellum width ( $\mu\text{m}$ )	Cribellum area ( $\mu\text{m}^2$ )
<i>M. dugesi</i> (5)	1.45 $\pm$ 0.30 [1.39]	4774 $\pm$ 578 [4263]	514 $\pm$ 16 [467]	44409 $\pm$ 4192 [37351]
<i>M. blandus</i> (5)	1.42 $\pm$ 0.57 [1.32]	4320 $\pm$ 290 [3753]	433 $\pm$ 18 [421]	32585 $\pm$ 2798 [30293]
<i>M. niveus</i> *(5)	1.02 $\pm$ 0.50 [1.16]	1794 $\pm$ 131 [2675]	315 $\pm$ 23 [362]	13229 $\pm$ 1361 [20943]
<i>M. pallidus</i> *(5)	1.10 $\pm$ 0.19 [1.15]	2109 $\pm$ 148 [2478]	318 $\pm$ 10 [349]	15378 $\pm$ 504 [19306]
<i>M. mians</i> (5)	1.28 $\pm$ 0.61 [1.18]	2983 $\pm$ 282 [2650]	382 $\pm$ 22 [368]	24281 $\pm$ 1680 [21598]
<i>M. pearcei</i> (5)	1.09 $\pm$ 0.54 [1.18]	2488 $\pm$ 147 [2650]	372 $\pm$ 18 [368]	21209 $\pm$ 1415 [21598]

Table 1: Mean values of carapace width, spigot number, and cribellum width and area  $\pm$  the standard error. Sample size given in parentheses, ancestral values in square brackets, species with a divided cribellum indicated by asterisks.



Figs. 4–6: Regression analyses of change (difference between the ancestral character state and the extant species character state) in spider carapace width and change in cribellum area (4), spigot number (5), and cribellum width (6). Circled points indicate those species with divided cribella, n = *Mallos niveus*, p = *M. pallidus*, r = *M. pearcei*, d = *M. dugesi*, b = *M. blandus*, m = *M. mians*.

the calamistrum passes over each half. A median cribellar division may also enhance cribellar thread stickiness by producing broader cribellar threads. The cribellar thread of an amaurobiid species with a divided cribellum consists of two parallel bands of cribellar fibrils, each presumably produced by one of the cribellum's plates (Eberhard & Pereira, 1993).

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