Changes in spinning anatomy and thread stickiness associated with the origin of orb-weaving spiders

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The cribellum is an oval spinning field whose spigots produce silk fibrils that form the outer surfaces of the primitive prey capture threads found in aerial spider webs. A comparison of the cribella and cribellar capture threads of 13 species of spiders representing seven families (Amaurobiidae, Desidae, Dictynidae, Filistatidae, Neelanidae, Oecobiidae, and Uloboridae) confirms that the stickiness of a cribellar thread is directly related to the number of spigots on a spider's cribellum. This comparison also demonstrates that the origin of orb-weaving spiders from ancestors that constructed less highly organized webs was associated with increases in both the weight-specific number of cribellum spigots and the weight-specific stickiness of cribellar prey capture threads. In contrast to other cribellate spiders, the number of cribellum spigots of orb-weaving species of the family Uloboridae scales to spider mass. Thus, the origin of orb-weaving spiders involved not only behavioural changes that stylized and restricted the placement of cribellar threads, but also included morphological changes that increased the stickiness of these capture threads by endowing them with more cribellar fibrils.

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ADDITIONAL KEY WORDS:—ancestor-reconstruction analysis – character evolution – cribellum – cribellar capture thread – web architecture.

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INTRODUCTION

The large infraorder Araneomorphae contains over 95% of all living spider species (Coddington & Levi, 1991). Its origin coincided with the appearance of both aerial spider webs designed to capture flying prey and sticky prey capture threads. By retaining insects, these capture threads enhance web performance by providing more time for a spider to locate, run to, and subdue an insect before it can escape from the web (Chacón & Eberhard, 1980; Craig, 1987; Eberhard, 1986, 1989, 1990). The first capture threads produced by spiders were cribellar threads (Figs 1, 2) whose dry, fuzzy surfaces are formed of thousands of fine, looped fibrils (Fig. 3) that are produced by the spigots (Fig. 4) of an oval spinning field termed the cribellum (Figs 5, 6; Eberhard, 1988; Eberhard & Pereira, 1993; Opell, 1993, 1994a, b, 1995; Peters, 1983, 1984, 1986, 1992). Each spigot of a spider’s cribellum contributes a single fibril to the cribellar thread. Thus, the number of cribellar spigots on a spider’s cribellum is the principal determinant of the stickiness of the thread that the spider produces (Opell, 1994a, b, 1995) unless it loops the completed strand before depositing it in the web (Opell, unpublished observations).

Cribellar capture threads persist in many types of webs, including webs whose threads radiate from a retreat (Fig. 7), funnel-webs (Fig. 8), sheet-webs of various types (Fig. 9), cob-webs (Fig. 10), and ray-webs (Fig. 11). These threads are found even in the orb-webs produced by members of the family Uloboridae (Fig. 12). This study examines changes associated with the origin of orb-weaving spiders by comparing the number of cribellum spinning spigots and the stickiness of the cribellar thread produced by non-orb-weaving spiders with those produced by cribellate orb-weavers.

The orb-web achieves its strength with comparatively little silk investment and contains spirally-arrayed capture threads supported by non-sticky radial lines (Fig. 12; Craig, 1987; Denny, 1976). Insights into some of the changes that may have been associated with the origin of the orb-web can be gained by examining changes that have occurred within the Orbiculariae, a clade that includes the orb-weaving spiders and their descendants. Two subclades comprise the Orbiculariae, the Deinopoidea and the Araneoidea. The Deinopoidea contains the cribellate orb-weaving family Uloboridae and the family Deinopoidea, whose members construct highly modified orb-webs (Coddington, 1986a; Coddington & Sobrevila, 1987). In contrast, the Araneoidea includes orb-weavers that have replaced cribellar threads with viscous adhesive threads. Within the Orbiculariae, the transition from cribellate orb-webs to adhesive orb-webs was marked by an increase in thread and web stickiness, relative to the weight of the spider that constructed the web (Opell, 1997,
1998). This transition suggests that an evolutionary premium is placed on the stickiness of an orb-web’s capture threads (Bond & Opell, 1998).

Within the family Uloboridae, orb-web reduction led to the triangle-webs constructed by members of the genus *Hyptiotes* and simple-webs constructed by members of the genus *Miagrammopes* (Lubin, 1986). These changes in web architecture are associated with a decrease in the total length of the web’s cribellar threads and are accompanied by a compensatory increase in the stickiness per mm of capture thread (Opell, 1994a, 1996). Consequently, the total stickiness that each web presents is, relative to spider weight, very similar. The increased stickiness of cribellar threads produced by spiders of similar size results from an increase in the number of spigots that form a cribellum (Opell, 1994b, 1995). Thus, the stickiness of the cribellar threads of orb-weaving uloborids appears not to be limited by spider size, but by the material and behavioural cost of producing cribellar threads. Together, these observations show clearly that capture thread stickiness is an evolutionarily malleable feature that has played a critical role in spider evolution.

Figures 1–6. Cribellar threads and cribella. Fig. 1. Cribellar thread of *Badumna longinqua* (scale bar = 100 µm). Fig. 2. Cribellar thread of *Waitkera waitakerensis* (scale bar = 100 µm). Fig. 3. Cribellar fibrils of *Matachia livor* (scale bar = 20 µm). Fig. 4. Cribellar spigots of *Badumna longinqua* (scale bar = 10 µm). Fig. 5. Entire cribellum of *Matachia livor* (scale bar = 200 µm). Fig. 6. Divided cribellum of *Badumna longinqua* (scale bar = 200 µm).
Figures 7–12. Prey capture webs that incorporate cribellar threads. Fig. 7. The radiating web of *Kukulcania hibernalis*. Fig. 8. The funnel-web of *Badumna longinqua*. Fig. 9. The suspended sheet-web of *Neolana pallida*. Fig. 10. The cob-web of *Mexitilia trivittata*. Fig. 11. The ray-web of *Matachia livor*. Fig. 12. The orb-web of *Waitkera waitakerensis*. All webs were dusted with corn starch to make their threads more visible for photography. As cribellar threads retain more corn starch, they are the most conspicuous threads in these webs.
The orb-web is one of the most complex structures made by an animal. Nevertheless, compared to non-orb-webs, an orb-web may be viewed as a type of reduced web because the highly stereotypic behaviour responsible for its construction restricts the placement of the web’s capture threads (Figs 7–12). Orb-weaving spiders may compensate for this apparent reduction in the amount of capture thread that their webs contain in several ways. The web’s planar architecture probably more effectively exposes its capture thread to prey and facilitates the spider’s quick response to prey that strike the web. The daily web renewal exhibited by many orb-weaving spiders (Carico, 1986; Opell, 1998) maintains web structure and ensures that capture threads are maximally sticky. Another factor may be an increase in the stickiness of the cribellar capture threads produced by orb-weaving spiders. Just as the reduced webs of uloborids have stickier cribellar threads than their orb-weaving ancestors, the cribellar threads of orb-webs should be, relative to spider mass, stickier than those of non-orb-webs. To achieve this greater stickiness, the cribella of these orb-weavers should have, relative to spider mass, more spigots than the cribella of non-orb-weaving spiders. This study tests these hypotheses in a phylogenetic context by using both the comparative method (Harvey & Pagel, 1991) and more traditional statistical analyses.

MATERIAL AND METHODS

Species studied

This study includes five orb-weaving species of the family Uloboridae and eight non-orb-weaving species that belong to six other families and collectively construct five different types of prey capture webs. To confirm the relationship between cribellum spigot number and cribellar thread stickiness, I also included four uloborid species that construct reduced webs (Lubin, 1986; Opell, 1994a, 1996): two triangle-web species of the genus Hyptiotes and two simple-web species of the genus Miagrammopes. Table 1 lists the species included in this study and Figure 13 shows their phylogenetic relationship. This summary phylogeny inserts the tree for the included species of Uloboridae, as established by Coddington (1990a), into the more inclusive phylogeny of Griswold et al. (1999).

Cribellum spigot number

This study included species with entire and divided cribella (Figs 5 and 6, respectively). I determined the number of spigots on a spider’s cribellum by first removing its cribellum and mounting it in water-soluble medium on a microscope slide. The cribellum was examined under a compound microscope equipped with differential phase contrast (Nomarski) optics. For entire cribella, I used a video camera and a computerized digitizing apparatus to measure the surface area of the cribellum and the density of approximately 50 spigots in three regions of the cribellum: anterior midline, lateral central region, and posterior lateral margin. I then computed the number of cribellum spigots by multiplying surface area by mean spigot density. For divided cribella, I measured the area of a single cribellar plate
and determined the density of spigots in the median, central, and lateral regions of this plate. The number of spigots on a single plate was then doubled to obtain the total number of cribellum spigots.

**Cribellar thread stickiness**

Capture threads were collected from webs on raised supports that were glued to microscope slides at 4.8 mm intervals. I used only recently spun threads that were

### Table 1. Spider masses, and cribellum features. Mean ± 1 SE. Ancestral values are in brackets. For spigot number, the first ancestral value is that used in examining the relationship between thread stickiness and spigot number and the second value is that used in examining the relationship between spider mass and spigot number. Values for Uloboridae are from Opell (1994b, 1996). Superscript numbers that follow species names designate values in Figures 16 and 17

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>(sample size)</th>
<th>mass (mg)</th>
<th>area per spigot (µm²)</th>
<th>cribellum area (µm²)</th>
<th>total spigot number</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Filistatidae</strong></td>
<td>Kakulama hibernalis</td>
<td>(16)</td>
<td>334.5 ± 36.1</td>
<td>4.6 ± 0.21</td>
<td>302 ± 18</td>
<td>7767 ± 271</td>
</tr>
<tr>
<td></td>
<td>(Hentz) radiating D</td>
<td></td>
<td>[212.7]</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Oecobiidae</strong></td>
<td>Platoseius floridanus</td>
<td>(32)</td>
<td>3.5 ± 0.2</td>
<td>4.9 ± 0.1</td>
<td>25 ± 1</td>
<td>317 ± 22</td>
</tr>
<tr>
<td></td>
<td>[91.0]</td>
<td></td>
<td>[49.4]</td>
<td></td>
<td></td>
<td>[±, 3783]</td>
</tr>
<tr>
<td><strong>Dictynidae</strong></td>
<td>Mexitila trivittata</td>
<td>(15)</td>
<td>21.1 ± 1.7</td>
<td>6.7 ± 0.2</td>
<td>312 ± 11</td>
<td>4716 ± 193</td>
</tr>
<tr>
<td></td>
<td>(Banks) cob</td>
<td></td>
<td>[4031]</td>
<td></td>
<td></td>
<td>[±, 3783]</td>
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<tr>
<td><strong>Amacrobidae</strong></td>
<td>Callobius havemani</td>
<td>(6)</td>
<td>87.7 ± 3.9</td>
<td>15.6 ± 0.6</td>
<td>403 ± 20</td>
<td>2614 ± 193</td>
</tr>
<tr>
<td></td>
<td>[70.5]</td>
<td></td>
<td>[±, 3449]</td>
<td></td>
<td></td>
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</tr>
<tr>
<td><strong>Neolaniidae</strong></td>
<td>Neolana pallida</td>
<td>(17)</td>
<td>51.9 ± 2.9</td>
<td>9.1 ± 0.1</td>
<td>166 ± 4</td>
<td>1835 ± 61</td>
</tr>
<tr>
<td></td>
<td>Forster &amp; Wilton sheet D</td>
<td></td>
<td>[74.5]</td>
<td></td>
<td></td>
<td>[4228, 3950]</td>
</tr>
<tr>
<td><strong>Desidae</strong></td>
<td>Matachia hieron</td>
<td>(16)</td>
<td>30.7 ± 2.6</td>
<td>5.2 ± 0.1</td>
<td>352 ± 19</td>
<td>6740 ± 267</td>
</tr>
<tr>
<td></td>
<td>(Urquhart)</td>
<td></td>
<td>[102.5]</td>
<td></td>
<td></td>
<td>[±, 2257]</td>
</tr>
<tr>
<td><strong>Badumna insignis</strong></td>
<td>(L. Koch) funnel D</td>
<td>(6)</td>
<td>295.7 ± 56.6</td>
<td>5.9 ± 0.3</td>
<td>630 ± 31</td>
<td>10878 ± 1011</td>
</tr>
<tr>
<td></td>
<td>(L. Koch) funnel D</td>
<td></td>
<td>[202.4]</td>
<td></td>
<td></td>
<td>[±, 2257]</td>
</tr>
<tr>
<td><strong>Badumna longipalpis</strong></td>
<td>(L. Koch) funnel D</td>
<td>(17)</td>
<td>208.9 ± 24.0</td>
<td>5.7 ± 0.2</td>
<td>533 ± 12</td>
<td>9552 ± 332</td>
</tr>
<tr>
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<td>(L. Koch) funnel D</td>
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<td>[202.4]</td>
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<td></td>
<td>[±, 2257]</td>
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<tr>
<td><strong>Uloboridae</strong></td>
<td>Waitkera waitakerensis</td>
<td>(35)</td>
<td>9.0 ± 0.5</td>
<td>8.2 ± 0.1</td>
<td>518 ± 5</td>
<td>3894 ± 74</td>
</tr>
<tr>
<td></td>
<td>(Chamberlain) orb</td>
<td></td>
<td>[14.3]</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td><strong>Sinarhaba referens</strong></td>
<td>(Muma &amp; Gertsch) orb</td>
<td>(22)</td>
<td>4.4 ± 0.2</td>
<td>6.4 ± 0.1</td>
<td>116 ± 2</td>
<td>1890 ± 31</td>
</tr>
<tr>
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<td>[14.3]</td>
<td></td>
<td>[±, 2257]</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Hyptiotes caeruleus</strong></td>
<td>(Hentz) triangle</td>
<td>(42)</td>
<td>7.76 ± 0.5</td>
<td>6.3 ± 0.1</td>
<td>453 ± 16</td>
<td>7278 ± 278</td>
</tr>
<tr>
<td></td>
<td>(Hentz) triangle</td>
<td></td>
<td>[±, 2257]</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Hyptiotes gertschii</strong></td>
<td>Chamberlin &amp; lvie orb</td>
<td>(34)</td>
<td>9.68 ± 0.5</td>
<td>5.6 ± 0.1</td>
<td>431 ± 9</td>
<td>7724 ± 174</td>
</tr>
<tr>
<td></td>
<td>[14.3]</td>
<td></td>
<td>[±, 2257]</td>
<td></td>
<td></td>
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</tr>
<tr>
<td><strong>Magrampompes anastatellus</strong></td>
<td>simple</td>
<td>(115)</td>
<td>5.26 ± 0.2</td>
<td>4.4 ± 0.03</td>
<td>390 ± 5</td>
<td>8990 ± 140</td>
</tr>
<tr>
<td></td>
<td>(Chickering) orb</td>
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<td>[14.3]</td>
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<td></td>
<td>[±, 2257]</td>
</tr>
<tr>
<td><strong>Magrampompes sp.</strong></td>
<td>simple</td>
<td>(25)</td>
<td>4.83 ± 0.3</td>
<td>5.3 ± 0.1</td>
<td>387 ± 8</td>
<td>7254 ± 165</td>
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<tr>
<td></td>
<td>(Hentz) triangle</td>
<td></td>
<td>[17.9]</td>
<td></td>
<td></td>
<td>[±, 2257]</td>
</tr>
<tr>
<td><strong>Octonoba sinensisin</strong></td>
<td>orb</td>
<td>(29)</td>
<td>9.4 ± 0.5</td>
<td>7.9 ± 0.1</td>
<td>371 ± 11</td>
<td>4717 ± 150</td>
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<td></td>
<td>(Walckenaer) orb</td>
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<td>[17.9]</td>
<td></td>
<td></td>
<td>[±, 2257]</td>
</tr>
<tr>
<td><strong>Ototyphlus flavus</strong></td>
<td>(Simon) orb</td>
<td>(50)</td>
<td>12.6 ± 0.6</td>
<td>8.9 ± 0.1</td>
<td>397 ± 15</td>
<td>4463 ± 138</td>
</tr>
<tr>
<td></td>
<td>[14.7]</td>
<td></td>
<td>[±, 2257]</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Philonyssa arizonica</strong></td>
<td>(Gertsch) orb</td>
<td>(26)</td>
<td>13.5 ± 0.9</td>
<td>6.4 ± 0.1</td>
<td>326 ± 10</td>
<td>5110 ± 168</td>
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<tr>
<td></td>
<td>[14.7]</td>
<td></td>
<td>[±, 2257]</td>
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<td>[±, 2257]</td>
</tr>
</tbody>
</table>
not contaminated by dust or pollen or damaged by a spider walking on them. These were collected from newly constructed orb-webs and from newly deposited capture lines of non-orb-weaving species. In the latter case, this was often facilitated by partially destroying a web and looking each morning for new threads. I measured the stickiness of capture threads from only five of the eight non-orb-weaving species included in this study. Individual capture threads could not be collected from the small webs of *Platoecobius floridanus* (Oecobiidae). I was unable to collect uncontaminated cribellar threads of sufficient length from *Callobius bennetti* (Amaurobiidae) in the field and these spiders did not build webs in an environmental chamber. *Mexitilia trivittata* (Dictynidae) individuals looped their cribellar threads before depositing them on a supporting foundation lines (Fig. 10) and these threads were not comparable to the linear threads of the other species included in this study (Figs 1, 2). *Kukulcania hibernalis* (Filistatidae) also deposited looped cribellar threads, but these threads could be removed from their supporting foundation lines (Eberhard & Pereira, 1993) and extended so that they became linear.

After a thread sample was taken, I collected and weighed the spider that produced it. I measured thread stickiness with a strain gauge that incorporated a glass or stainless steel needle (Opell, 1993, 1994a). A contact plate made from a 2 mm wide piece of 320 grit, 3M waterproof silicon carbide sandpaper was glued to the tip of this needle. The particles on the surface of these sandpaper plates are uniform in size and distribution (Opell, 1993) and these plates registered the same stickiness for cribellar threads as did contact plates made from fleshfly (*Sarcophaga bullata* Parker).
wings (Opell, 1994a). Thus, for both cribellar and adhesive capture thread, a sandpaper contact plate registers stickiness values similar to that of a representative insect surface.

A motorized advancement mechanism pressed the cribellar thread against a sandpaper contact plate at a constant speed (15.5 mm/min for threads from orb-webs and 10.7 mm/min for threads from non-orb-webs) until a force of 19.61 μN/mm of thread contact was achieved. The thread was then immediately withdrawn by this mechanism at a constant speed (14.0 mm/min for threads from orb-webs and 10.4 mm/min for threads from non-orb-webs) until it pulled free from the contact plate. The force registered by the strain gauge immediately before this occurred was divided by the contact plate’s width (measured to the nearest 20 μm) to yield stickiness, expressed as μN of force per mm of thread contact with the sandpaper plate. The stickiness of four thread samples was measured for each specimen and their mean was used as a spider’s value.

Table 2 gives the mean temperature and the percent relative humidity at which the stickiness of each species’ thread was measured. This table also gives the mean precision of these stickiness measurements, as determined by the sensitivities of the needles used in their measurement and the exactness with which their position on a linear scale could be read. Mean relative humidity, mean absolute precision, and mean percent precision sensitivity (expressed as a percentage of the mean stickiness of the species measured) were normally distributed for both orb-weaving and non-orb-weaving species (Shapiro–Wilk-W-Statistic $P > 0.05$). T-tests show that these values do not differ between orb-weaving and non-orb-weaving species ($P > 0.05$). However, absolute precision was only marginally insignificant ($P = 0.052$), with values for non-orb-weavers being greater than those for orb-weavers.

The standard error of the mean stickiness of four different sectors of a spider’s thread provides an index of the uniformity of these measurements (Table 2). However, this value is not in the strict sense a measure of repeatability because measuring the stickiness of a span of thread alters its surface properties and tension, and precludes a second measurement of this strand from being taken. Duplicate measurements of an individual’s thread may differ for at least three reasons: (1) thread features may not be absolutely uniform along the length of a thread, (2) cribellar threads are not symmetrical around the axial fibres and may present a slightly different surface area or configuration to a contact plate depending on their rotation, and (3) although the particles on the surface of sandpaper contact plates have a very uniform size and distribution (Opell, 1993), the number and configuration of the particles that a thread contacts varies slightly from measurement to measurement. These factors are not simply artifacts of the technique employed in this study, as they also affect the strength with which capture threads hold insect surfaces. Therefore, the mean of the four stickiness measurements of an individual spider’s thread provides a more representative value of the thread’s typical performance than does a single stickiness measurement.

**Phylogenetic analysis**

To confirm the relationship between cribellum spigot number and cribellar thread stickiness and to evaluate the relationship between spider mass and cribellum spigot number, I employed the ancestor-reconstruction method described by Huey &
Table 2. Spider masses, and cribellar thread stickiness. Mean ± 1 SE. Ancestral values are in brackets. For non-orb-web species, the ancestral stickiness value used with spigot number precedes that used with spider mass. Uloboridae are from Opell (1994b, 1996). The stickiness of uloborid cribellar threads were measured at 23° ± 2°C.

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Sample size</th>
<th>Mass (mg)</th>
<th>Stickiness (µN/mm)</th>
<th>Measurement precision (µN/mm (% species X))</th>
<th>Measurement uniformity (µN/mm (% species X))</th>
<th>Temperature (°C)</th>
<th>Relative humidity (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Filistatidae</td>
<td>Kukulcania hibernalis</td>
<td>(14)</td>
<td>327.8 ± 35.5 [231.9]</td>
<td>22.67 ± 2.49 [19.64, 18.30]</td>
<td>1.15 (5.3%)</td>
<td>5.33 (23.5%)</td>
<td>23.0 ± 0.2</td>
<td>60.4 ± 0.3</td>
</tr>
<tr>
<td>Neolaniidae</td>
<td>Neolana pallida</td>
<td>(17)</td>
<td>51.8 ± 3.0 [136.0]</td>
<td>5.52 ± 0.67 [13.29, 13.93]</td>
<td>1.01 (18.3%)</td>
<td>1.88 (34.1%)</td>
<td>24.2 ± 0.4</td>
<td>70.2 ± 1.3</td>
</tr>
<tr>
<td>Desidae</td>
<td>Matachia livor</td>
<td>(17)</td>
<td>33.4 ± 2.5 [124.3]</td>
<td>22.83 ± 2.11 [17.78, 17.98]</td>
<td>1.14 (5.0%)</td>
<td>5.53 (24.2%)</td>
<td>24.3 ± 0.5</td>
<td>72.5 ± 0.9</td>
</tr>
<tr>
<td></td>
<td>Badumna insignis</td>
<td>(6)</td>
<td>295.7 ± 56.6 [203.6]</td>
<td>20.42 ± 2.66 [17.09, 17.17]</td>
<td>2.01 (9.8%)</td>
<td>2.66 (13.0%)</td>
<td>25.5 ± 0.5</td>
<td>76.3 ± 2.9</td>
</tr>
<tr>
<td></td>
<td>Badumna longinga</td>
<td>(15)</td>
<td>190.7 ± 17.0 [203.6]</td>
<td>13.52 ± 1.99 [17.09, 17.17]</td>
<td>1.30 (9.9%)</td>
<td>3.97 (29.3%)</td>
<td>26.2 ± 0.3</td>
<td>71.6 ± 0.8</td>
</tr>
<tr>
<td>Uloboridae</td>
<td>Waitkera waitakerensis</td>
<td>(38)</td>
<td>9.0 ± 0.5 [14.68]</td>
<td>15.45 ± 0.82 [14.68]</td>
<td>1.37 (8.9%)</td>
<td>3.07 (19.9%)</td>
<td>—</td>
<td>68 ± 0.3</td>
</tr>
<tr>
<td></td>
<td>Siratoba referena</td>
<td>(25)</td>
<td>4.4 ± 0.2 [14.68]</td>
<td>11.66 ± 0.61 [14.68]</td>
<td>1.78 (15.3%)</td>
<td>1.66 (14.2%)</td>
<td>—</td>
<td>66 ± 0.4</td>
</tr>
<tr>
<td></td>
<td>Hyptiotes cavatus</td>
<td>(56)</td>
<td>8.11 ± 0.57 [26.38]</td>
<td>26.18 ± 1.70 [26.38]</td>
<td>1.73 (7.4%)</td>
<td>5.37 (22.9%)</td>
<td>—</td>
<td>58 ± 0.2</td>
</tr>
<tr>
<td></td>
<td>Hyptiotes gertschi</td>
<td>(32)</td>
<td>9.83 ± 0.56 [26.78]</td>
<td>29.84 ± 2.17 [26.78]</td>
<td>1.78 (5.9%)</td>
<td>6.82 (22.7%)</td>
<td>—</td>
<td>55 ± 0.4</td>
</tr>
<tr>
<td></td>
<td>Miagrammopes animotus</td>
<td>(101)</td>
<td>4.96 ± 0.23 [26.75]</td>
<td>31.50 ± 1.78 [26.75]</td>
<td>1.69 (5.6%)</td>
<td>5.53 (18.5%)</td>
<td>—</td>
<td>62 ± 0.4</td>
</tr>
<tr>
<td></td>
<td>Miagrammopes species</td>
<td>(24)</td>
<td>3.75 ± 0.24 [26.75]</td>
<td>21.41 ± 2.07 [26.75]</td>
<td>1.78 (7.2%)</td>
<td>5.74 (23.3%)</td>
<td>—</td>
<td>65 ± 0.4</td>
</tr>
<tr>
<td></td>
<td>Uloborus glomosus</td>
<td>(30)</td>
<td>9.4 ± 0.5 [17.12]</td>
<td>13.50 ± 1.08 [17.12]</td>
<td>2.86 (18.5%)</td>
<td>4.02 (25.9%)</td>
<td>—</td>
<td>56 ± 0.1</td>
</tr>
<tr>
<td></td>
<td>Octonoba sinensis</td>
<td>(35)</td>
<td>12.7 ± 0.7 [16.40]</td>
<td>17.12 ± 1.21 [16.40]</td>
<td>2.68 (15.7%)</td>
<td>4.22 (24.7%)</td>
<td>—</td>
<td>55 ± 0.1</td>
</tr>
<tr>
<td></td>
<td>Philoponella arizonica</td>
<td>(27)</td>
<td>13.4 ± 0.9 [16.40]</td>
<td>14.97 ± 1.11 [16.40]</td>
<td>1.78 (11.9%)</td>
<td>2.55 (17.0%)</td>
<td>—</td>
<td>66 ± 0.3</td>
</tr>
</tbody>
</table>
Bennett (1986, 1987) and summarized by Harvey & Pagel (1991). I first determined the probable ancestral values of each species’ features using the rooted minimized sum of squared changes option in the continuous character tracing section of the MacClade 3.02 phylogenetic program (Maddison & Maddison, 1992). I then calculated the changes from these ancestral states to those expressed by each species and examined the relationships between these changes using regression statistics. The values for all species for which cribellum spigot number and cribellar thread stickiness values were available were used to examine the functional relationship between these features. To examine relationships between spider mass and the number of cribellum spigots and between spider mass and cribellar thread stickiness, I performed separate ancestral-reconstruction analyses for orb-weaving species and non-orb-weaving species. Tables 1 and 2 give the inferred ancestral values used in these analyses.

RESULTS

Cribellum spigot number and cribellar thread stickiness

Table 1 gives the number of spigots on each species’ cribellum, and Table 2 gives the stickiness of each species’ cribellar thread. Both change in cribellum spigot number and change in cribellar thread stickiness are normally distributed (Shapiro–Wilk-W-Statistic $P > 0.24$). Change in cribellar thread stickiness is directly related to change in cribellum spigot number (Fig. 14). This confirms for a broader taxonomic sampling the findings of Opell (1994b, 1995) that the number of spigots on a spider’s cribellum is the principal determinant of cribellar thread stickiness.

Before the phylogeny of Griswold et al. (1999) was available, I used the phylogeny
of Coddington and Levi (1991) to examine the relationship of thread stickiness to the number of cribellum spigots. This analysis also showed that thread stickiness is directly related to spigot number ($Y = 0.002X - 0.005$, $r^2 = 0.51$, $P = 0.004$), suggesting that this relationship is robust and not likely to change with future phylogenetic emendations.

**Spider mass and cribellum spigot number**

For both orb-weaving species and non-orb-weaving species, change in spider mass and change in spigot number are normally distributed (Shapiro–Wilk-W-Statistic $P > 0.27$). For the eight non-orb-weaving species, there was no relationship between change in spigot number and change in spider mass ($F = 3.62$, $P = 0.106$). However, for the five orb-weaving species, this relationship was significant ($F = 11.34$, $P = 0.044$; Fig. 15).

Had the relationship between change in spigot number and change in spider mass been significant for non-orb-weaving species, the hypothesis that the origin of orb-weaving spiders was marked by an increase in cribellum spigot number could have been tested by comparing the slopes and intercepts of these regression lines. As this was not possible, the number of spigots per mg of spider mass of these species was compared.

**Mass-specific cribellum spigot number**

For three species, spigot number per mg spider mass was not normally distributed (Shapiro–Wilk-W-Statistic $P < 0.05$). When log$_e$ transformed, this index was normally distributed for all species except *Badumna insignis* (Desidae) ($P = 0.03$). As the mean
value of this species is among the four smallest values for non-orb-weavers. I judged that this single case of non-normality would not compromise the conclusions made from a parametric statistical comparison of these values. An ANOVA showed that log₁₀ spigot number per mg differed among species ($F=260.69$, $P=0.0001$). A Ryan Q test (alpha = 0.05; Day & Quinn, 1989) showed that the log₁₀ spigots per mg of orb-weaving species was greater than that of non-orb-weaving species (Fig. 16). The mean value of the non-orb-weaving species’ means was 102.2 spigots/mg and that of orb-weaving species was 445.4 spigots/mg. For non-orb-weaving species, species means were not normally distributed (Shapiro–Wilk-W-Statistic $P<0.05$). A Kruskal–Wallis Test showed that these grand means differed (Chi Sq = 8.47, $P=0.003$).

\[ F = 0.94, \quad P = 0.40, \quad r^2 = 0.24 \]

Thus, the regression line for the relationship between spider mass and thread stickiness that has been established for cribellate orb-weaving spiders (Opell, 1998) cannot be compared to that of non-orb-weaving spiders. Instead, the hypothesis that the origin of orb-weaving spiders was marked by an increase in thread stickiness will be tested by comparing the stickiness per mg of spider mass for the species studied.

**Mass-specific cribellar thread stickiness**

Stickiness per mg spider mass was normally distributed (Shapiro–Wilk-W-Statistic $P>0.05$) for only three species, but became so for all species when log₁₀ transformed
Figure 17. Comparison of the stickiness per mg of spider mass for non-orb-weaving and orb-weaving spiders. Error bars denote ±1 standard error. Letters refer to similar mean values of log_n stickiness/mg spider mass as determined by a Ryan Q test (alpha = 0.05).

(P > 0.11). An ANOVA showed that log_n stickiness per mg differed among species (F = 155.62, P = 0.0001. A Ryan Q test (alpha = 0.05) showed that the log_n stickiness per mg spider mass of orb-weaving species was greater than that of non-orb-weaving species (Fig. 17). The mean value of the non-orb-weaving species’ means was 0.22 μN/mm/mg, whereas that of orb-weaving species was 1.83 μN/mm/mg. For non-orb-weaving species, species means were not normally distributed (Shapiro–Wilk-Statistic P < 0.05). A Kruskal–Wallis Test showed that these grand means differed (Chi Sq = 6.81, P = 0.009).

Changes in mass-specific spigot number and thread stickiness

Like histograms of mass-specific cribellar spigot number (Fig. 16) and mass-specific cribellar thread stickiness (Fig. 17), changes in the inferred ancestral values of these indices show that both have increased markedly in the orb-weaving lineage (Fig. 18). To statistically evaluate these differences, I subtracted the ancestral value from the values of extant species to determine if the average change of orb-weaving species exceeded that of non-orb-weaving species. I made this comparison using both the ancestral node for all species included in this study (N 1 in Fig. 18) and the ancestral node shared by orb-weaving species and their sister clade (N 2 in Fig. 18). I excluded *Hyptiotes* and *Miagrammopes* species from these analyses for two reasons. First, it has already been established that web reduction within the Uloboridae is associated with increases in cribellar spigot number and cribellar thread stickiness (Opell, 1994a, b). Second, including these species would inflate the changes in mass-specific spigot number and thread stickiness for the orb-weaving lineage and render the test of the hypothesis that these changes were associated with the origin of this lineage less conservative.
Figure 18. Ancestral values for mass-specific cribellar spigot number and cribellar thread stickiness. The values for each species appear below its name. Ancestral values, as determined by the rooted minimized sum of squared changes option in the continuous character tracing section of the MacClade 3.02 phylogenetic program (Maddison & Maddison, 1992), appear at each node. As stickiness was not measured for all species, the ancestral values for mass-specific stickiness were computed using a pruned cladogram.

For non-orb-weaving species, changes in mass-specific cribellar spigot number and mass-specific cribellar thread stickiness were not normally distributed (Shapiro-Wilk W-Statistic $P < 0.05$). Therefore, I compared the mean values of orb-weaving and non-orb-weaving species using a Wilcoxon 2-sample test. When the ancestral value at node 1 was used, the mean change in the number of cribellar spigots per mg spider mass for orb-weaving species was $+357.7$ and for non-orb-weaving species $+12.8$. This difference was significant ($Z = 2.85$, $P = 0.004$). When the value at node 2 was used the value for orb-weaving species was $+204.0$ and for non-orb-weaving species $-135.6$, a difference that was also significant ($Z = 2.65$, $P = 0.008$). For node 1, the mean change in stickiness per mg spider mass for orb-weaving species was $+1.41$ and for non-orb-weaving species $-0.21$, a difference that was significant ($Z = 2.54$, $P = 0.011$). For node 2, the value for orb-weaving species was $+1.05$ and for non-orb-weaving species $-0.70$, a difference that was also significant ($Z = 2.10$, $P = 0.036$).


The results of this study support the hypothesis that the origin of orb-weaving spiders was associated with an increase in the weight-specific stickiness of the cribellar capture thread that was facilitated by an increase in the weight-specific number of cribellum spigots. On average, orb-weaving uloborids have, relative to spider mass, 4.4 times more spigots on their cribella than do non-orb-weavers and produce cribellar threads that are 8 times stickier. This study also confirms the direct relationship between cribellum spigot number and cribellar thread stickiness (Opell, 1994b, 1995) using a greater number and diversity of species. Among orb-weaving species of the family Uloboridae, but not among the eight other cribellate species, the number of cribellum spigots scales to spider mass. This too may be a feature associated with the origin of orb-weaving spiders. However, it is possible that within other cribellate families more extensive sampling may also show a similar scaling of cribellum spigot number to spider mass.

Many of the features of non-orb-webs and orb-webs remain to be compared. However, when combined with the architectural differences between these web forms, the greater stickiness of the cribellar threads of orb-weaving spiders has the potential to reduce the cost of web production while maintaining a web’s ability to retain prey. The capture threads of orb-webs are deposited in a regular, spiral array (Fig. 12) and the daily web replacement that characterizes many orb-weaving spiders (Opell, 1998) serves both to renew a web’s structure and to ensure that its capture threads are fresh and maximally sticky. Thus, relative to a spider’s size, these threads could be more widely spaced than those of non-orb-webs (particularly those of funnel and sheet-webs, such as shown in Figs 8 and 9) and still maintain the same stickiness per cm² of capture area. Consequently, shorter lengths of capture thread would be required to maintain the same capture area and this could reduce the behavioural and material cost of web construction, particularly when coupled with the silk recycling that is associated with web replacement by orb-weaving spiders (Opell, 1998). Data on the total silk cost, total stickiness, total capture area, and longevity of different web forms are needed to test this hypothesis.

**Limits on cribellar thread stickiness**

It is principally the number of spinning spigots on a spider’s cribellum that determines the stickiness of the capture thread that it produces (Opell, 1994a, b, 1995, this study). Some spiders increase this primary stickiness by looping a cribellar thread as it is deposited (Opell, unpublished observations). However, like an increase in the number of cribellar spigots, this results in the expenditure of more silk per unit length of capture thread. Consequently, the stickiness of a cribellar capture thread appears to be limited ultimately by the number of fibrils that it contains and by the cost of producing these fibrils. Morphological constraints on cribellum size do not appear to limit the stickiness of cribellar threads produced by most spiders. The cribella of orb-weaving species have many more spigots relative to spider mass than do non-orb-weaving species. However, the actual number of spigots that these orb-weavers possess is only half that found in species of the reduced-web genus
Miagrammopes that have both smaller masses and narrower abdomens (Opell, 1994b) than orb-weaving uloborids. Thus, the number of cribellar spigots that a spider's abdomen can accommodate does not seem to be highly constrained morphologically. Because the abdomens of small orb-weaving species could accommodate at least twice as many cribellar spigots as they actually have, and because spigot number increases as approximately the square of cribellum dimensions, it seems clear that larger non-orb-weaving species could support cribella with many more spigots than they actually possess. Thus, it appears that the requirements of capture thread stickiness, coupled with the cost of producing cribellar thread, are key factors that influence the number of spigots on a spider's cribellum.

Web architecture, longevity and placement

The benefits of producing stickier cribellar thread appear to be affected by both web architecture and web longevity. As cribellar capture thread is costly to produce (Opell, 1997, 1998), selection for stickier thread is most likely to occur when two conditions are met. First, a web’s architecture must fully expose its capture thread to potential prey. Second, relative to spider mass, the ratio of an orb-web’s total stickiness to its total cost should at least as great as that of a non-orb-web. This latter comparison must account for the frequent replacement of orb-webs when compared with the longer duration of most cribellate non-orb-webs.

The planar design of an orb-web fully exposes its capture threads to flying prey. However, the orb-web is inherently prone to damage. The daily removal and replacement of at least large parts of the orb-web (Carico, 1986) that appears to be a plesiomorphic feature of the Orbiculariae (Opell, 1998), resolves this problem and maintains both the physical integrity and stickiness of the web. Unless a web is exposed to a great deal of dust or pollen, the stickiness of its capture threads diminishes very slowly over the course of a day. Additionally, the practice of many orb-weavers of ingesting silk as they take down their webs and of recycling this silk in subsequent webs significantly improves the economy of orb-web production (Opell, 1998). These conditions would seem to favour the direct relationships between spider mass or size and both orb-web stickiness (Opell, 1996, 1997, 1999) and orb-web capture area (Opell, 1999; Sherman, 1994).

In contrast to orb-webs, some regions of most non-orb-webs seem less fully exposed to potential prey than other regions. Additionally, many non-orb-webs are constructed gradually and sometimes in segments over a period of many days (Eberhard, 1987; Opell, unpublished observations) and appear to have a greater and more variable longevity than orb-webs (Opell, unpublished observations). These characteristics probably reduce the stickiness of cribellar threads found in non-orb-webs, render their total stickinesses and capture areas less predictable than those of orb-webs, and make it less likely that these web features will scale to spider mass as do those of orb-webs (Opell, 1996, 1997, 1999).

Many non-orb-web spiders construct webs that remain in place for extended and indefinite periods. These spiders expand and repair their webs, but they appear to exhibit no regular pattern of web replacement (Eberhard, 1987; Opell, unpublished observations). Consequently, web capture area and stickiness are in a state of flux. Cribellar threads in the older, more central regions of funnel- and sheet-webs, such as those produced by Badumna (Desidae) and Neolana (Neolanidae) species (Figs 8,
Thread stickiness and the origin of orb-weaving spiders

9), are typically contaminated with dust and are not very sticky, whereas threads at the perimeter of the web and in recently repaired areas are fresh and sticky (Opell, unpublished observations). Radiating thread networks produced by **Kukulcania** (Filistatidae) and **Mexitilia** (Dictynidae) (Figs 7, 10) are also characterized by a mixture of older, less sticky threads and newer, stickier threads. Even the radiating webs of the genus **Matachia** (Desidae) (Fig. 11) do not appear to be replaced at predetermined intervals (Opell, unpublished observations).

**Differences among non-orb-weaving species**

Of the non-orb-weaving species studied, **Mexitilia trivittata** and **Matachia livor** construct webs with the most restricted placement of cribellar threads (Figs 10, 11). The architectures of these webs are not as highly stereotypic as that of an orb-web and the phylogenetic positions of these two species (Fig. 13) make it unlikely that either web form is the precursor of the orb-web. However, the presence of more widely-spaced and shorter lengths of capture threads in their webs suggests that the features of their cribella and cribellar threads should be more similar to those of orb-weaving species than the other non-orb-weaving species included in this study. The results of this study support this prediction. **Mexitilia trivittata** and **M. livor** have a greater number of cribellum spigots per mg of spider mass than do the other six non-orb-weaving species (Fig. 16). **Matachia livor** has greater stickiness per mg of spider mass than the other four non-orb-weaving species (Fig. 17). **Mexitilia trivittata** also produces very sticky cribellar threads (Opell, unpublished observations). This is attributed in part to the number of spigots on its cribellum and in part to the cribellar thread being looped before it is deposited in the web.

**Conclusion**

This study includes representatives of some of the major forms of spider prey capture webs. There are both other web forms and other variants of the web forms studied. However, this sampling shows clearly that changes in the stickiness of the prey capture threads of these webs played an important role in the diversification of spider foraging modes. The behavioural changes responsible for these different web forms were accompanied by morphological changes in the spider’s cribellum that altered the stickiness of the web’s cribellar capture threads. The direct relationship between cribellum spigot number and capture thread stickiness appears to facilitate these changes. It appears that increased thread stickiness is favored as the placement of capture threads becomes more restricted or more widely spaced within the web, and as part or all of the web is replaced more frequently.

This study focuses on changes in web architecture that favor increased cribellar thread stickiness. However, as the cribellum is a plesiomorphic feature of the spider infraorder Araneomorphae, the many ecribellate members of this clade that lack a cribellum have arrived at this condition by adapting prey capture modes that do not rely on cribellar capture threads. Differences in the size and shape of the cribellum within members of cribellate families and genera also make it likely that some groups have evolved less sticky cribellar threads. The evolutionary plasticity of the cribellum is documented by a number of families, genera, and even species.
pairs (putative sister species) that have both cribellate and ecribellate members (Forster, 1970; Forster & Wilton, 1973). This study suggests that the stickiness and cost of a web’s capture threads are important features in the economy and ecology of web use. Orb-web architecture effectively exposes these capture threads and favors an increase in their stickiness. However, this does not signify that cribellate orb-webs, or even the adhesive orb-webs derived from them are the single best web form. Compared with the cribellate orb-webs included in this study, the adhesive orb-webs constructed by members of the Araneoidea clade achieve both a greater total stickiness relative to spider mass and a greater stickiness per cm² capture area at no increase in the material cost of producing the web’s capture threads (Opell, 1997, 1999). Despite even these refinements in orb-web design, about 60% of orbicularian species produce webs whose architectures differ markedly from the group’s plesiomorphic orb-web form (Griswold et al., 1998). These web forms include simple, radiating thread arrays, sheet-webs, and cob-webs, some of which are at least superficially similar to the webs of cribellate spiders (Griswold et al., 1998). This trend away from orb-web architecture may not be as surprising as it at first seems. In reviewing orb-web function, Eberhard (1990) concludes from records of prey capture that “orbweavers clearly tend to be general predators.” If this assessment is correct, then one of the main avenues of evolution open to members of this clade is to construct webs that allow them to specialize on a particular type (guild, taxon, size, or behavioural characteristic) of insect, or to forage effectively in a particular microhabitat.

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